is fairly successful for a variety of liquids over extended pressure, compression and viscosity ranges, and yields physically reasonable predictions.

The empirical Vogel-Tammann-Fulcher (VTF) equation, $\log \eta = A + B/(T - T_0)$, is an excellent representation for the temperature-dependent viscosity data of glycerol over 12 orders of magnitude[22], where T_0 is roughly the Kauzmann temperature[23] (at which the liquid and crystal are isentropic). A modified form of the VTF equation, in which T_0 is assumed to depend linearly on P, has been used to fit high-pressure conductivity[24,25] and Brillouin scattering data[26] but does not describe our viscosity data. Following the assumption that the parameters A and B are constants[24,25], independent of both pressure and temperature, then the isothermal high-pressure viscosity data can be used with the VTF equation to calculate $T_0(P)$. Applying the ambient-pressure result[22] that $T_g = T_0 + 55$ K, we obtain $T_g(P)$ as shown in Fig. 4. This plot has several important features. First, the resulting $T_g(P)$ are nonlinear with pressure and agree with estimates from high-pressure measurements of heat capacity and dielectric constant[6,8]. Such nonlinearity is not widely recognized but was theoretically predicted[32] and has been seen for other liquids[27]. We do, however, find a linear relationship between T_0 and volume (inset to Fig. 4).

Alternatively, one can assume that A and the ratio B/T_0 are constant, as found for methanol over a limited pressure range[28]. This leaves unaltered the nonlinear behaviour of $T_0(P)$, but now $T_g - T_0$ must increase with pressure to agree with experimental data. The nearly linear relationship between T_0 and volume is preserved. The key difference between these two models is whether the fragility parameter B/T_0 (ref. 20) is independent of pressure. This parameter is related to the rate of structural breakdown in the liquid above T_g and is used for the classification of glass-forming liquids. But past studies have not addressed its pressure dependence. Evaluation of this requires variable-temperature, high-pressure data, and the single available viscosity point for glycerol[9] suggests that B/T_0 is independent of pressure. This suggests that the combined effects of temperature and pressure on glycerol are such that an isothermal crossing of T_g, at any pressure, would yield a constant configurational entropy change. Further data are clearly required to clarify this issue. □

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Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source

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ARCTIC tundra has been a net sink for carbon dioxide during historic and recent geological times[1-4], and large amounts of carbon are stored in the soils of northern ecosystems. Many regions of the Arctic are warmer now than they have been in the past[5-10], and this warming may cause the soil to change from a carbon dioxide sink to a source by lowering the water table[11,12], thereby accelerating the rate of soil decomposition (CO_2 source)[3,13-15] so that this dominates over photosynthesis (CO_2 sink). Here we present data indicating that the tundra on the North Slope of Alaska has indeed become a source of carbon dioxide to the atmosphere. This change coincides with recent warming in the Arctic, whether this is due to increases in greenhouse gas concentrations in the atmosphere or to some other cause. Our results suggest that tundra ecosystems may exert a positive feedback on atmospheric carbon dioxide and greenhouse warming.

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The current, recent and future carbon flux of terrestrial ecosystems is controversial[16,17], and at present, the carbon budget does not balance, implying uncertainty as to the current terrestrial carbon flux. It may be that over the past 30-40 years, the terrestrial biosphere has been a net sink for carbon[11,18] large enough to account for the 'missing carbon' injected into the atmosphere and not accounted for in oceanic uptake or atmospheric storage[19,20]. Analyses by Tans *et al.*[17] concluded the likelihood of a net terrestrial sink with high-latitude CO_2 sources to the atmosphere.

Northern ecosystems contain up to 455 Gt (petagrams) of C in the soil active layer and the upper levels of the permafrost, or up to ~60% of the ~750 Gt C currently in the atmosphere as CO_2 (refs 1-4). Arctic tundra ecosystems alone contain more than 50 Gt C below ground as dead organic matter. In the historic and recent geological past, rates of carbon accumulation in tundra worldwide have been ~0.1-0.3 Gt C per year[2-4,12,21,22]. Tussock tundra is estimated to have accumulated carbon at the rate of 23 g C m^{-2} yr^{-1} (0.02 Gt C per year worldwide), wet tundra at the rate of 27 g C m^{-2} yr^{-1} (0.03 Gt C per year worldwide[2,4]) to 40-120 g m^{-2} yr^{-1} (refs 24, 25).

High-latitude ecosystems are expected to undergo the greatest increases in surface temperature with a doubling of atmospheric CO_2. Surface temperature increases of 4 °C in summer and as much as 17 °C in winter have been predicted for high northern latitudes[5,23], providing the potential for large absolute and relative increases in temperature in arctic regions. The importance of permafrost, ice and snow in controlling arctic ecosystem processes also makes the Arctic particularly sensitive to warming[24].

Regional warming of surface air temperatures[5-8] and permafrost temperatures[9,10] has been experienced over arctic Alaska and Canada and/or central Siberia over the past century. In Alaska, despite complications from heat island effects at

Barrow[26], regional summer warming over the past 70 and 20 years at Barrow and Prudhoe Bay, respectively, seems to be reflected in their temperature records (Fig. 1) and agrees with the general trend in global temperature deviations[27-29]. But although the direction of the change observed on the north slope of Alaska is that predicted by general circulation models and climate reconstructions, the temperature rise cannot definitely be ascribed to greenhouse warming[30].

Here we report measurements of whole-ecosystem CO_2 flux measured over five seasons (1983–1985, 1987, 1990) at Toolik Lake and along a latitudinal transect in 1990, from the Arctic Ocean at Prudhoe Bay to Toolik Lake, Alaska (Fig. 2). The initial measurements (1983–1985, 1987) were made at Toolik Lake using a closed, CO_2 and long-term temperature-controlled, null-balance greenhouse chamber (CO_2LT chamber) system[31]. During the summer of 1990, we made diurnal and seasonal measurements of ecosystem CO_2 flux along a north-south transect from the Arctic Ocean at Prudhoe Bay to Toolik Lake, 200 km to the south, using a portable ecosystem cuvette and gas exchange system[32].

The repeated summer measurements of diurnal CO_2 flux at Toolik Lake made between 1983 and 1987 indicated a loss of CO_2 from the tussock tundra of 0.72–3.9 g C m^{-2} d^{-1} (Table 1). If we assume a nominal active season of 125 days, these annual rates of CO_2 efflux varied from 53 to 286 g C m^{-2} yr^{-1}, reflecting the year-to-year variability in environmental conditions (Table 1). We may have slightly underestimated CO_2 loss by missing some periods of soil and plant respiration in early spring and late autumn (S. A. Zimov, personal communication).

Diurnal and seasonal patterns of carbon flux were dominated by periods of carbon loss to the atmosphere. For example, Happy Valley shows a seasonal increase in the rate of loss of carbon at 'night' from early season to peak season. This increase is presumably due to increasing soil temperatures, soil aeration and depth of thaw over this period. Peak net ecosystem carbon uptake also increases from early to mid-season, but on no days measured is the carbon balance positive, and soil decomposition and plant respiration always exceed photosynthetic uptake for the diurnal period. By mid-season, despite increases in midday rates of carbon uptake, carbon loss has increased more than has photosynthetic uptake, and the net loss of carbon has increased compared to early season rates. The measurement period was extended in 1991 to cover almost the entire snow-free period, reducing the extrapolation necessary (W.C.O., unpublished data). The results support those presented here and confirm the carbon loss from spring snow melt to autumn freeze-up along the transect measured.

Net seasonal carbon loss to the atmosphere was found at all sites measured. Carbon loss to the atmosphere during the 1990 season generally increased from north to south (Fig. 2), and on the drier areas within a site (Fig. 2, Table 1). The site closest to the coast, Prudhoe Bay Wet, was the wettest site measured (Table 1). The southern tussock tundra sites, Toolik Lake and Happy Valley, were better drained, and had greater thaw depths

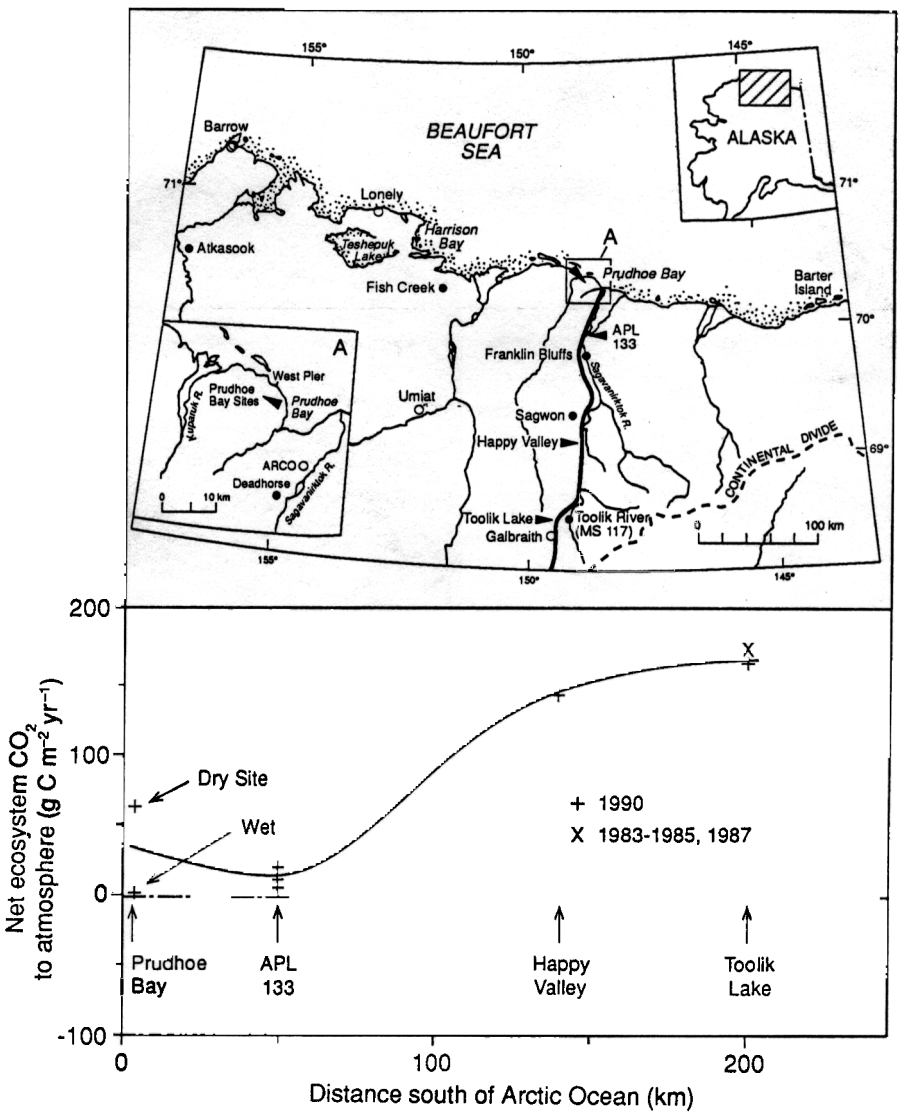

FIG. 1 Mean annual summer (June through August) temperatures from 1921 to 1990 at Barrow Alaska and from 1970 to 1990 at Prudhoe Bay Alaska. Represented are 3-yr sliding mean values from the U.S. Weather Service for Barrow, Alaska and from ARCO for the ARCO airport tower at Prudhoe Bay, Alaska.

TABLE 1 Characteristics of research sites and measured CO_2 fluxes

Site	Latitude	Longitude	Distance (km)	Elevation (m)	Tundra type	Moisture	Year	Average summer temperature* (°C)	Summer precipitation* (mm)	Average CO_2 flux ($g\,C\,m^{-2}\,d^{-1}$)
Prudhoe Bay wet	70° 22′	148° 45′	2.5	3	Wet sedge	Wet	1990	6.5¶	49§	+0.034
Prudhoe Bay moist	70° 22′	148° 45′	2.5	3	Wet sedge	Moist	1990	6.5¶	49§	+0.66
APL-133 control	69° 50′	148° 45′	50	80	Wet/moist sedge	Moist	1990	10.0‡	69‡	+0.216
APL-133 flooded	69° 50′	148° 45′	50	80	Wet/moist sedge	Wet	1990	10.0‡	69‡	+0.091
APL-133 drained	69° 50′	148° 45′	50	80	Wet/moist sedge	Moist	1990	10.0‡	69‡	+0.39
Happy Valley	69° 08′	148° 50′	140	366	Tussock	Moist	1990	13.1†	50†	+1.155
Toolik Lake	68° 38′	149° 35′	200	732	Tussock	Moist	1990	9.3‡	160‖	+1.34
Toolik Lake							1983	8.9#	N.D.**	+3.8
Toolik Lake							1984	N.D.**	264‖	+3.9
Toolik Lake							1985	7.5‡; 6.5#	213‖	+1.1
Toolik Lake							1987	9.2§	246‖	+0.72

Positive values of flux indicate CO_2 loss to the atmosphere. Daily CO_2 flux measurements are calculated from diurnal measurements, and the integrated seasonal uptake is averaged to provide an average daily flux for the period of biological activity.

* Summer months from June–August.

† This study, missing 22 days of data.

‡ Toolik River, MS-117 (D. Kane, personal communication).

§ This study.

‖ Toolik River, MS-117 (R. J. McClure, personal communication).

¶ National Climatic Data Center, Asheville, NC computed from the mean minimum and mean maximum recorded temperatures.

Toolik River, MS-117 (R. H. Haugen, personal communication).

** N.D. Not Determined.

and lower water tables. The average rate of annual CO_2 loss for the tussock tundra sites in 1990 was $156\,g\,C\,m^{-2}\,yr^{-1}$, whereas carbon loss for the wet coastal tundra sites (Prudhoe Bay and APL 133-3) was $\sim 34\,g\,C\,m^{-2}\,yr^{-1}$ (Table 1). The results for the tussock tundra ecosystems during the 1990 sampling season agree well with the initial measurements made between 1983 and 1987 (Table 1) and with subsequent measurements made in 1991 and 1992 (W.C.O., unpublished data). These data indicate a change in carbon balance of the tundra with respect to the atmosphere, in response to the trend in climate warming for the north slope of Alaska.

We feel that the change from carbon accumulation to carbon loss in these ecosystems is not caused directly by the increase in temperature but indirectly, by enhanced drainage and soil aeration, and a decrease in the water table[11,12]. Decomposition of the soil organic layer in northern peatlands is controlled much more by drainage, and consequently soil aeration, than by temperature[3,13–15]. Warmer periods in the past that resulted in peat accumulation in the Canadian sub-arctic and Alaskan arctic[33], where there is no evidence of current carbon accumulation[3], are thought to reflect the combination of warmer and wetter conditions.

Given the general pattern of warming for the north slope of Alaska and the Canadian arctic[6–10,34], the patterns observed along this transect in Alaska may be widespread and the carbon loss huge. If the average rate of loss in tussock tundra of $156\,g\,C\,m^{-2}\,yr^{-1}$ is typical for circumpolar tussock tundra, the loss of carbon to the atmosphere in 1990 from the $0.90 \times 10^6\,km^2$ of tussock tundra worldwide[2] would be 0.14 Gt C per year. Similarly, if the $34\,g\,C\,m^{-2}\,yr^{-1}$ of CO_2 evolution from wet tundra is applied to the $1.00 \times 10^6\,km^2$ of wet coastal tundra, another 0.03 Gt C is lost annually to the atmosphere. Adding 0.02 Gt C for efflux from arctic tundra lakes and rivers[35] results in a total estimated annual loss of 0.19 Gt C from these three circumpolar arctic surface types. This combined efflux can be compared to the 0.2–0.7 Gt C calculated to be lost to the atmosphere from high-latitude ecosystems[17]. Given the large below-ground stores of carbon in arctic, boreal forest and high-latitude bogs, these high-latitude ecosystems could provide a considerable positive feedback on increasing atmospheric CO_2 and global warming.

There are many uncertainties in predicting the long-term effect of global change on arctic ecosystems. The initial response to warming and drying may be a loss of carbon from the system,

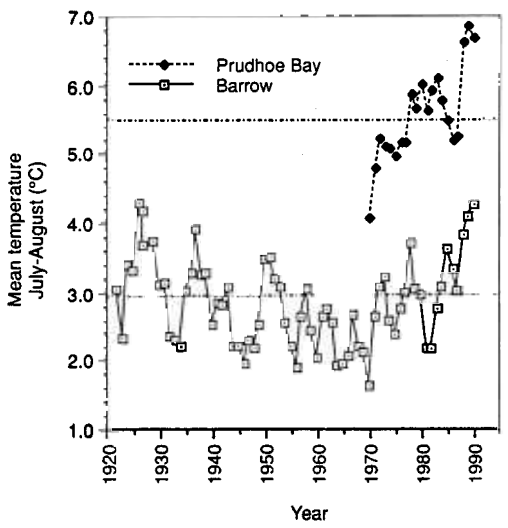

FIG. 2 Site locations on the north slope of Alaska. From north to south: Prudhoe Bay, APL-133, Happy Valley, Toolik Lake (upper panel). Seasonal carbon dioxide flux (as carbon) along a latitudinal gradient from Prudhoe Bay to Toolik Lake, Alaska in 1990 (+), and for four additional years of measurement at Toolik Lake (1983–1985, 1987; ×). The line represents an interpolation of values for 1990. Mean flux for 1983–85 and 1987 is $175 \pm 62\,g\,C\,m^{-2}\,yr^{-1}$ (mean ±1 s.e.). Site differences in soil moisture are noted at Prudhoe Bay and APL 133. The three values at APL 133 represent the three areas of differing moisture availability (drained, control and impounded) studied which resulted in higher, medium and lower CO_2 efflux from the tundra to the atmosphere respectively. For the initial measurements (1983–85, 1987), there were three replicate control chambers running under ambient conditions. Measurements were made every 3 minutes, and averaged and recorded every 6 minutes throughout the day and the season. For 1990, measurements were made from shortly after snow melt to shortly before soil freeze-up in the autumn at each site on each of six replicate plots roughly once every 1.5 h throughout the 24-h measurement period. Seasonal flux was extrapolated to zero at the time of snow melt in the spring and of soil freeze-up in the autumn. The net seasonal flux for each site was determined as the integral under the curve of the seasonal pattern of daily fluxes. There was little variability in daily CO_2 flux rates among the replicates at each site on any day. Because these measurements were made only during the snow-free summer period, they underestimate the seasonal carbon loss to the atmosphere by the presumably small amount of soil and plant respiration that occurs under snow during the unmeasured winter period.

whereas at longer intervals, invasion by shrub and tree species may result in increased above-ground carbon storage. Other compensatory processes include cooling of the soil surface (following increased insulation from drying of the soil surface and litter or biomass accumulation from elevated CO_2 and/or other climatic effects). Currently there is no evidence that these compensatory processes are acting or will act quickly. Field and laboratory experiments indicate little or no stimulation of photosynthesis in the Arctic by elevated atmospheric CO_2 (ref. 36). It is likely that global warming will lead to significant outgassing of carbon from wet and moist tundra before other processes reincorporate this carbon into arctic areas. Global warming could accelerate the rate of carbon loss in arctic tundra ecosystems by increasing the depth of thaw, increasing soil drainage and aeration, and increasing rates of soil decomposition and plant respiration more than gross primary productivity.

The recent climate patterns may be part of the normal climate variation or an early indication of greenhouse warming. In either case, it is clear that they have affected the current carbon flux from the arctic ecosystem, and that arctic and boreal forest ecosystems could provide a strong positive feedback on atmospheric carbon dioxide concentration. □

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The transient response of terrestrial carbon storage to a perturbed climate

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MODEL simulations suggest that at equilibrium, global warming driven by higher atmospheric concentrations of greenhouse gases will lead to increased terrestrial carbon storage[1,2], implying a negative feedback between the global vegetation/soil system and the atmospheric CO_2 concentration. But changes in vegetation and soil type that result in a net release of CO_2 to the atmosphere (such as those caused by wildfires) could be more rapid than changes that result in a net increase in terrestrial carbon storage (such as species immigration and soil formation), so that in its transient response to climate change, the terrestrial vegetation/soil system could be a net source of carbon to the atmosphere. Here we use two general circulation models[3,4] to estimate the transient response of the terrestrial surface to a step doubling of atmospheric CO_2. We find that vegetation and soil changes could prove to be a significant source of CO_2 in the first 50–100 years following a climate warming, increasing the atmospheric CO_2 concentration by up to a third of the present level.

Several estimates have been made for the carbon reserves of the terrestrial surface[5,6]. These estimates are obtained by classifying the vegetation and soils, and then multiplying area estimates for each classification category by the carbon concentration of soil and vegetation in research sites typical of that category. Vegetation and soil classifications have also been related to climate variables and used in assessments of possible global responses to climate changes[1,2,7], for example to estimate changes in potential terrestrial carbon storage. Such calculations presumably estimate a long-term equilibrium response to a climate change. In the case of a 'greenhouse gas' climate warming, the long-term response of the terrestrial surface is to store more carbon[1,2].

Here we extend the methodology used by Smith *et al.*[2] to estimate the transient terrestrial surface response to a step change in climate. In brief, the method of determining present and future carbon reserves was this. (1) Expected current global distributions of vegetation were mapped at a $0.5° \times 0.5°$ (latitude and longitude) resolution using the Holdridge life-zone classification[8] and a climate database of monthly precipitation and temperature[9]. (2) Estimates of carbon storage per unit area for each Holdridge life zone[2] were derived for above-ground biomass using data from Olson *et al.*[5] and for soil carbon from Post *et al.*[10]. These estimates were applied to the map produced in step 1 to obtain global terrestrial-surface carbon pools[2]. (3) Simulations of current ($1 \times CO_2$) and $2 \times CO_2$ climates from the general circulation models developed by the Goddard Institute for Space Studies[3] and the Geophysical Fluid Dynamics Laboratory[4] were used to construct climate change schemes[2]. (4) The climate database was altered according to the changes implied by the climate-change schemes, and steps 1 and 2 (above) were repeated to obtain estimates of carbon storage (presumably after a long period of equilibration) for the altered climate conditions.

To obtain an estimate of the change in source–sink relations between the terrestrial surface and the atmosphere, we developed a simple compartment model of terrestrial carbon reserves (above-ground biomass and soils) and applied this model to the globally mapped vegetation changes in response to the two climate-change schemes. The compartment model used in this analysis parallels the approach used in current